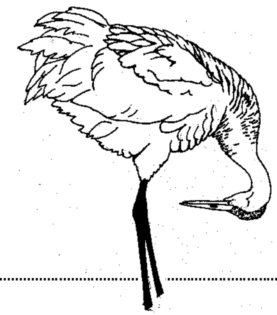
Reproductive Physiology



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Cranes differ physiologically from the more commonly studied avian species by exhibiting an **incomplete annual molt**, **low reproductive rate**, and **delayed sexual maturity**. Cranes appear to be especially **susceptible to stress** from physical and behavioral disturbance, unfamiliar territories, and disease. Although mature cranes normally reproduce annually, they may experience one or more years of reduced productivity apparently due to stress (Mirande et al. 1988 unpubl.). Unfortunately, little is known specifically about crane reproductive physiology; what little we do know indicates that cranes function like other birds.

In some ways most birds, including cranes, can tolerate environmental insults better than mammals. For example, some foods which are toxic to mammals provide good nutrition for birds. Breakdown products of food absorbed from the intestines are shunted through the liver and kidneys where **toxic products are removed** before reaching the general circulation (Sturkie 1954, 1986; Duke 1986). In another area, although cranes have long, exposed legs, they can withstand cold extremes by using **counter current circulation** in the tibiotarsus to conserve body heat and prevent hypothermia by warming blood returning from the feet (Whittow 1986). Unlike mammals, cranes (and all other birds) are better adapted to stave off dehydration because they excrete nitrogenous wastes as semi-solid **urates** instead of urea. This mechanism conserves body water that would be required to carry away the urea (Grimminger and Scanes 1986).

Cranes and swans possess a unique anatomical feature; the **trachea is coiled and** posteriorly **embedded** in the bony mass of the sternum (Pettingill 1970). The amount of tracheal coiling varies by species with the Gray Crowned Crane possessing the least coiled and the Japanese Crane the most highly coiled trachea. Some authors relate the coiled and elongated trachea to sound amplification, other authors believe it decreases skeletal mass, and still others relate it to thermoregulation (Prange et al. 1985; Gaunt et al. 1987).

In the following, we emphasize crane physiology. The references in Table 7.1 provide additional details on avian physiology.

Reproduction

Cranes generally mate for life (Walkinshaw 1973), but they do replace mates that die and some mate swapping has been reported (Littlefield 1981; E. Kuyt, Department of Environment, Edmonton, Canada, personal communication). Cranes begin laying when

TABLE 7.1

Avian physiology references.

Topic	Reference
Environmental, ecological	Farner et al. 1971
General, molt	Farner et al. 1972
Light, photorefractoriness	Farner et al. 1983
Incubation, domestic fowl	Landauer 1967
Molt	Lucas and Stettenheim 1972a, 1972b
Reproduction, behavior	Lofts and Murton 1973
General, light, reproduction	Marshall 1960
Season, reproduction, migration	Marshall 1961a, 1961b
Endangered species	Martin 1975
Reproductive cycles	Murton and Westwood 1977
Reproductive anatomy and physiology, domestic fowl	Nalbandov 1958
General, anatomy	Pettingill 1970
General, reproduction	Skutch 1976
Incubation	Stromberg 1975
Anatomy and physiology, domestic fowl	Sturkie 1986
Incubation, domestic fowl	Taylor 1949

3-5 years old (Walkinshaw 1973; S. A. Nesbitt, Florida Game and Fresh Water Fish Commission, Gainesville, Florida, personal communication), but there are exceptions in captivity and in the wild (see Chapter 3; Radke and Radke 1986).

Reproduction is controlled by an **integrated neuroendocrine system** (Kobayashi and Wada 1973; van Tienhoven 1980; El Halawani et al. 1982; Oksche 1983). To use an analogy, the system functions like a symphony orchestra. The brain and related neural systems conduct the orchestra and the endocrine organs, gonads, and accessory reproductive organs produce the music. Like the conductor's eyes and ears, the bird's visual, tactile, olfactory, auditory, and other neural sensory elements relay environmental and body conditions, so the brain, more specifically the hypothalamus and pituitary, can control reproductive functions.

Light entrains endogenous physiological rhythms, especially production and release of luteinizing hormone releasing hormone (LHRH), to time the reproductive effort (Wingfield et al. 1981; Wada 1984; Gwinner and Dittami 1985; Farner 1986; Hiatt et al. 1987). By their presence or absence, rainfall, humidity, and a variety of other **environmental and behavioral factors** can either induce or thwart reproduction (Marshall 1961a, 1961b; Ghosh and Banerjee 1983; Wingfield 1985; Vleck and Priedkalns 1985; Bluhm 1985a). Behavioral interactions (e.g., presence of mate or territorial encounters with conspecifics) lead to increased or decreased reproductive development (El Halawani et al. 1980, 1982; Ottinger 1983; Bluhm 1985b).

Feedback mechanisms on the central nervous system effecting control of reproduction include endocrine products from the **pituitary**, **target hormones** (from reproductive organs), and **non-target hormones**. **Other feedback factors** are less understood and include refractory periods, target tissue exhaustion, and entrainment of **endogenous rhythms**. The brain and pineal show obvious **endogenous rhythms** while helping to control the release of inhibiting or releasing factors in the hypothalamus (Kobayashi and Wada 1973; Gorbman et al. 1983; Ueck and Umar 1983). The hypothalamus, deep at the base of the brain, acts as the reproductive coordinator. The brain senses surrounding conditions, integrates information from the internal milieu, and uses neural and chemical pathways to signal the **hypothalamus** to turn on or off production of **releasing or inhibiting factors** (Wingfield 1980).

The hypothalamus is not only controlled by higher neural centers in the brain, but also through **feedback mechanisms** from within the rest of the body. The hypothalamus produces the following **releasing or inhibiting factors**: LHRH, thyrotropin-releasing hormone (TRH), prolactin-inhibiting factor (PIF), somatostatin, growth-releasing factor (GRF), and corticotropin-releasing factor (CRF) (Kobayashi and Wada 1973; El Halawani et al. 1982; Farner 1986). Table 7.2 provides the specific function, signs, and effects of the hypothalmic and pituitary hormones that control reproduction.

The **gonadotropins** are produced and released in response to LHRH (Bluhm et al. 1983; Bluhm 1985a) (Fig. 7.1, Cycle 1). The ratio of follicle stimulating hormone (FSH) to luteinizing hormone (LH) released from the pituitary in response to LHRH stimulation differs and is dependent on the circulating levels of gonadal steroids (androgens, estrogens, and progestins) (Cusick and Wilson 1972; Davies et al. 1976; Cheng and Balthazart 1982; Gorbman et al. 1983; Scanes 1986). In a **basic feedback mechanism**, **increased** plasma levels of **FSH and LH** lead to **increased gonadal steroid** levels, and eventually (Fig. 7.1, Cycle 3) the **elevated steroid levels decrease LHRH** release (Temple 1974; Pavgi and Chandola 1981; Lal and Thapliyal 1985; Groscolas et al. 1986; Sharp et al. 1986; Hiatt et al. 1987).

Somatostatin, which is secreted from the pancreas and small intestine, inhibits release of growth hormone and is an important component in carbohydrate metabolism. Arginine vasotocin and isoleucine oxytocin (mesotocin) are produced by **neurosecretory neurons** located in the hypothalamus. Vasotocin and oxytocin are stored in the pituitary (posterior lobe) before release (Kobayashi and Wada 1973; Gorbman et al. 1983).

Male

The reproductive system in both sexes of cranes **regresses in the summer and fall** and **develops** again the next **spring**. Generally, male cranes produce **semen** at least one year **earlier** than females produce eggs. For example, 80% of captive male Whooping Cranes (12 of 15) produced semen by three years of age, but only 13% of captive female Whooping Cranes (2 of 15) lay eggs by five years of age (Ellis et al. 1992). A healthy, well-fed crane may be **reproductively active** each breeding season for its **entire adult life** (60 or more years).

FIGURE 7.1

Hormonal Control of the Crane Reproductive Cycle*

CYCLE 1 (WINTER)

Hypothalamus
LHRH release starts reproductive cycle**

Pituitary
LHRH starts FSH and LH release

Gonads
FSH and LH start androgen and estrogen production

Actions
Androgens and estrogens interact with hypothalamus and pituitary endocrine functions
Androgens and estrogens help control ratio of FSH to LH released from pituitary
Accessory reproductive organs start growth
Spermatogenesis and oogenesis begin

**elevated corticosterone levels can reduce LHRH release and interrupt cycle*

CYCLE 2 (SPRING)

Hypothalamus
LHRH release continues
Releases a variety of other factors

Pituitary
LH to FSH ratio increased
LH notably cyclical
Other hormones develop cyclic patterns

Gonads
Spermatogenesis and semen production fully established
Androgen production elevated
Ovulatory cycle established
Estrogen, progesterone, and prostaglandin levels cycling

Actions
Territories established, eggs and semen produced, and Nest building
Hormones interact with hypothalamus, begin decreasing LHRH release
Hormones interact with pituitary reducing FSH and LH release and increasing prolactin release
Relationships between cyclical peaks of corticosterone and prolactin change

CYCLE 3 (SUMMER)

Hypothalamus
LHRH release declines
Bird may recycle, return to Cycle 2 levels, cyclical patterns start to level off

Pituitary
Prolactin levels up while most other levels decline

Gonads
Gonadal regression
Steroid levels decline

Actions
Feed back from elevated hormone levels in Cycle 2 reduces LHRH
Incubation and brooding phase
Accessory reproductive organs regress

CYCLE 4 (FALL)

Hypothalamus
LHRH and other reproductively active levels of releasing factors minimal

Pituitary
FSH and LH levels minimal
Non-reproductive endocrinology predominates

Gonads
Inactive
Minimum estrogen and androgen levels

Actions
Family groups join social flocks

**A simplified view, see standard avian reproductive physiology texts for more detail.*

TABLE 7.2

Hypothalamic and pituitary control of reproduction.

Hormone[1]	Source	Production Effects	Function	Production Signs
LHRH	hypothalamus	elevates LH, FSH and corticosterone; elevates gonadal steroids	adenohypophysis response dependent on circulating androgens, estrogens, and progestins. LHRH release dependent on temporal peaks of prolactin and corticosterone	control of seasonal reproduction gonad and accessory reproductive development
TRH	hypothalamus	stimulates thyrotropin, growth hormone, and prolactin	controls metabolic rate; promotes or inhibits reproductive development; stimulates growth hormone	thyroxin production can effect reproduction, effect in cranes unknown
PRF	hypothalamus	stimulates prolactin	release dependent on prolactin and serotonin levels	induces broodiness, stops egg production
PIF	hypothalamus	inhibits prolactin	role unclear in birds	—
Somatostatin	pancreas and small intestines	inhibits growth hormone	helps control carbohydrate metabolism	—
GRF	hypothalamus	stimulates growth hormone	controls growth	—
CRF	hypothalamus	stimulates corticosterone	seasonal cycling of diurnal release patterns	may help control onset and termination of breeding
Arginine vasotocin	hypothalamus neurosecretory neurons, stored neurohypophysis	—	interacts with prostaglandins; important in controlling water balance	—
isoleucine oxytocin (mesotocin)	hypothalamus neurosecretory neurons, stored neurohypophysis	—	same as above	oviposition
FSH	adeno-hypophysis	LHRH stimulates; response dependent on circulating levels of androgens, estrogens, and progestins	increase seasonal levels of androgens, estrogens, progestins, and prostaglandins	spermatogenesis or ovary growth, elevates gonadal steroids, initiates reproductive growth
LH	adeno-hypophysis	LHRH stimulates; response dependent on circulating levels of androgens, estrogens, and progestins	increased seasonal levels of androgens, estrogens, progestins, and prostaglandins	ovulation, gonadal steroid production (especially androgens and progestins), initiates reproduction
Thyrotropin	adeno-hypophysis	—	elevates growth hormone, elevates thyroxin	helps control metabolic rate, may affect crane reproduction

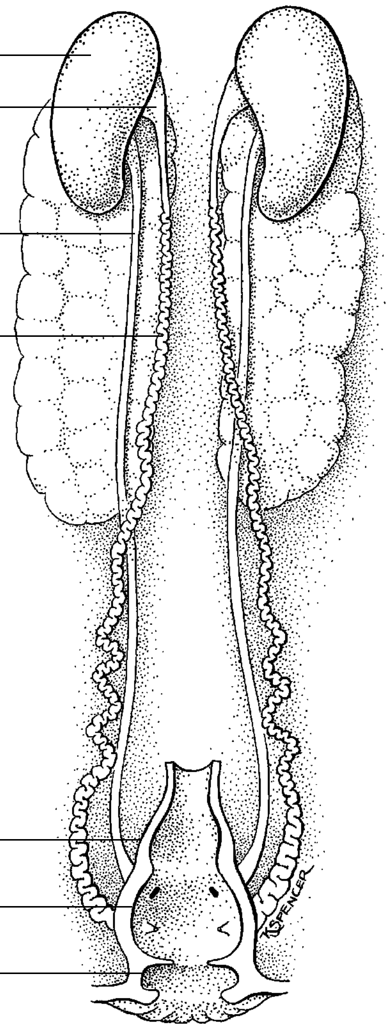
TABLE 7.2 CONTINUED

Hormone[1]	Source	Production Effects	Function	Production Signs
prolactin	adeno-hypophysis	PRF elevates prostaglandin E, increases secretion rate; release stimulated by serotonin and decreased by prolactin levels	LHRH release dependent on temporal peaks of prolactin and corticosterone	induces broodiness, stops egg production
ACTH	adeno-hypophysis	elevated corticosterones response to stress, ovulation, mineral corticoids and glucocorticoids	—	integral part of seasonal reproduction, stunts growth
growth hormone	adeno-hypophysis	somatostatin, decreases GRF, increases serotonin	increases free fatty acids for energy, reduces glucose utilization	induces growth, inhibits reproduction
serotonin	adeno-hypophysis, GI tract, adrenal gland, thymus neurohormone of wide distribution	stress and digestion stimulate production	elevates prolactin (acting on pituitary), decreases growth hormone (acting on hypothalamus)	—
Thyroxin	thyroid	TRH elevates	inhibits or promotes gonadal development, may be species or sex dependent	reproduction effect in cranes unknown
Androgens	gonads	aggressive encounters elevate release; helps control ratio of FSH and LH released, LH stimulates release	aids estrogen effect in ovulation and reproductive cycling	determines female rank in dominance hierarchy; cyclical in egg formation
Estrogens	gonads, especially developing follicles	FSH and LH stimulates, especially LH	oviduct growth, maturation, and maintenance; helps control ratio of FSH and LH released; elevates progestins	deposition of body fat and medullary bones, secondary sexual characteristics, sexual behavior, ova developmental cycling
Progestins	growing follicles especially just before and after ovulation	stimulated by FSH and especially LH, stimulated by estrogen	growth of oviduct and albumin secretion	ova developmental cycling
Prosta-glandins	gonads, oviduct	vasotocin interaction unclear, elevated in follicle just before oviposition	induces muscle contractions, closely related to essential fatty acid metabolism	induces oviposition
Corti-costerone	adrenal	stress increases related	diurnal peaks part of ovulatory cycle, LHRH releases dependent on temporal peaks of prolactin and corticosterone	elevated levels interfere with reproduction

[1] *LHRH = luteinizing hormone-releasing hormone, TRH = thyrotropin-releasing hormone, PRF = prolactin-releasing factor, PIF = prolactin inhibitory factor, GRF = growth hormone-releasing factor, CRF = corticotropin-releasing factor, FSH = follicle-stimulating hormone, LH = luteinizing hormone, ACTH = adrenocorticotropin.*

FIGURE 7.2

Male reproductive tract.



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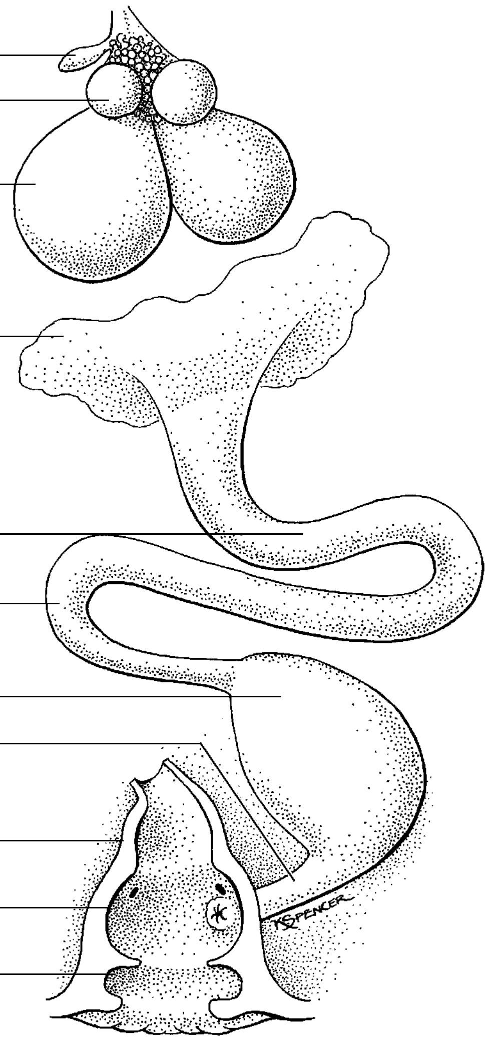
The crane's reproductive tract (Fig. 7.2) resembles that of the domestic fowl but is larger (Johnson 1986a, 1986b). By locating the terminal papilla of the vas deferens in the urodeum (middle chamber of the cloaca), one can **sex** reproductively active cranes. Male cranes possess a rudimentary phallus and ejaculatory groove in the cloaca; therefore, **copulation** is completed by cloacal contact with the everted cloaca of the female (Gee 1983).

The crane stores **semen** in the distal vas deferens and releases it when stimulated. Components of the ejaculate (sperm, other cells, and lymph) come from the seminiferous tubules within the testes, the cells lining the vas deferens, and from the lymph folds in the cloaca. Cranes do not produce specialized **accessory seminal fluids** like some other birds (Quay 1967; Lake 1981; King 1981). In the domestic chicken, spermatids may be released into the seminiferous tubule lumen early in its regeneration phase. After regeneration and early in the reproductive season, the seminiferous tubules in most birds are full of spermatids. Sperm cells mature from the spermatids and **accumulate** in the much convoluted **vas deferens** before ejaculation (Sturkie 1965; Lake 1981; Johnson 1986b). The entire process, from spermatid to sperm, takes 10 to 15 days in domestic fowl during the height of the reproductive season (Johnson 1986b). A spermatozoa takes one to four days to pass through the vas deferens (Munro 1938). In the Japanese Quail (*Coturnix coturnix japonica*), Jones and Jackson (1972) estimated that the entire process requires ca 25 days. For cranes, this duration is unknown.

FIGURE 7.3

Female reproductive anatomy (Florida Sandhill Crane)



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Female

With increasing daylight in the spring, the **ovary** and **oviduct** develop on the left side of the peritoneal cavity (Fig. 7.3). The ovary contains thousands of oocytes and several developing ova. With the chicken, the mature oocyte, also known as the **yolk,** contains about 51% water, 33% lipid, and 16% protein (Johnson 1986a). As for all birds, crane ovaries contain more oocytes than will ever be needed. The developing **ovum** is highly vascularized with only the central stigma containing a lesser number of arteries and veins on the exterior surface. Just before ovulation, the stigma blanches (blood flow stops and the blood drains out of the area), and the stigma ruptures releasing the ovum. Only a few ova are developing at any one time, and one is always larger than the rest (follicular hierarchy). Follicles that become yolk filled, but are not ovulated, are reabsorbed.

In chickensandcranes,the **eggproductioncycle** beginswiththeenlargementofseveraloocytesinto ova (follicularmaturation). In chickens, a descending size hierarchyisobviousinthelargestthreeor four ova.Thethreelargestfollicles(F_1-F_3) have different endocrinological responsibilities.Thelargestfollicle (F_1) produces **progesterone** and **prostaglandins** before andimmediatelyfollowing ovulation(Hertelendyetal. 1974; Dayand Nalbandov 1977; Poyserand Pharm 1981).Thethird largestfollicle(F_3) producesthelargest quantitiesof **estrogens** and releasesthehormonein dailycyclesto support thegrowthofthelargestfollicle (Huanget al. 1979; Kamiyohkiand Tanaka 1983; Wang and Bahr 1983; Johnson 1986a). The endocrinological functions of the second largest follicle (F_2) are intermediate between F_1 and F_3. In cranes, which lay one to three egg clutches (Sijuade 1978; Wylie 1978; Blossom 1984; see Chapter 3 for details), these events may differ from poultry with large multi-egg clutches.

Each segment of the oviduct (see Johnson 1986a for details) serves a function in the process of fertilization and egg production. Sperm penetration of the ova occurs in the infundibulum and **fertilization** occurs in the magnum. The albumen is added while the egg passes through the **magnum**. The inner and outer shell membrane are added to the egg in the **isthmus** where (in the chicken) the embryo reaches the 4 to 8 cell stage (Patterson 1910; Olsen 1942; Eyal-Giladi and Kochav 1976; Kochav et al. 1980). The egg is completed in the **shell gland** or uterus where salts and water are added to expand the egg within the shell membranes. About three quarters of the time needed for egg formation is spent in the shell gland. In the chicken, the embryo has reached the blastocyst stage containing about 60,000 cells when the egg is laid.

Cranes take 3-4 days to **form eggs**. The period between ovulation and oviposition in Sandhill and Red Crowned Cranes is **55-60 hours**. **Shell** formation takes about **45 hours** and is equal to the rate of calcium deposition in chickens (about 250 mg per hour) (M. S. Putnam, University of Wisconsin, Madison, Wisconsin, personal communication). Cranes produce one to three eggs per clutch and may produce several clutches per season if the preceding clutches are lost. **The number** of eggs produced may be **increased** if eggs are **removed as laid,** but the clutch interval will be less predictable. Cranes will stop producing eggs if eggs are added to the nest (Lack 1933).

Endocrinology

A series of complex endocrinological and behavioral events **begins weeks before the production of eggs and semen** (Fig. 7.1, Cycle 1) (Haase et al. 1976; El Halawani et al. 1980, 1982). The sequence for cranes remains to be determined, but is probably similar to those in other birds. In reproductively active Sandhill Cranes, the gonad mass and size increase, and estrogen and testosterone levels rise in the spring. Gonad weight, testosterone and estrogen increase in nonproductive adults but less than in reproductively active cranes (Tacha et.al. 1985). The sequence begins with **rising levels of LHRH** (Fig. 7.1, Cycle 1) which stimulates the **release of gonadotropins** (FSH and LH) from the pituitary (Cheng and Balthazart 1982; Bluhm et al. 1983; Scanes et al. 1983; Silverin 1984; Bluhm 1985a; Scanes 1986). Thereafter, LHRH and other components of the reproductive cycle support reproductive development in both sexes (Fig. 7.1). LH controls gonadal secretion of estrogens and androgens (Nalbandov 1958; Murton and Westwood 1977; Maung and Follett 1978).

The actions of **estrogens and androgens** appear to be the result of interactions with environmental and social cues to induce proper sexual behavior (Cheng 1974; Hutchinson 1975; Slater 1978; Donham 1979; Dittami 1981; Akesson and Raveling 1983; Bluhm et al. 1983; Bluhm 1985a, 1985b). **Androgens**, produced primarily by the ovary, are important to the normal cyclic phenomenon **associated with egg production**. The **LH surge** associated with ovulation is always preceded by an androgen rise (van Tienhoven 1980; Kamiyoshi and Tanaka 1983; Johnson 1986a). Androgens may also be responsible for rank in a female dominance hierarchy (Hohn and Cheng 1967). Androgen levels in both sexes of some birds rise in response to aggressive and territorial encounters, while in other birds, it is the rising androgen levels which increase aggressive encounters (Adkins-Regan 1981; Akesson and Raveling 1983; Wada 1983; Wingfield 1984a, 1984b, 1985; Wingfield et al. 1987).

Progesterones are secreted by the follicles throughout the reproductive period. Secretions of progesterone by the preovulatory follicle increase from a low level two to three days before ovulation to a peak several hours after ovulation (Shahabi et al. 1975; van Tienhoven 1980; Bahr et al. 1983; Kamiyoshi and Tanaka 1983; Johnson 1986b). Progesterone is important to the **growth and function of the oviduct** and acts on the oviduct to **increase secretion of albumen**.

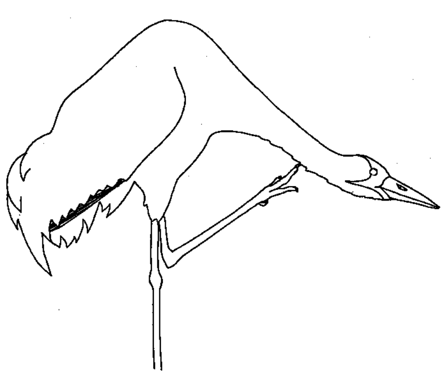
Plasma **prostaglandins and vasotocin** increase to their highest levels before **oviposition** (Day and Nalbandov 1977; Poyser and Pharm 1981; Johnson 1986a). Prostaglandins begin to rise in the preovulatory follicle about six hours before ovulation and continue to rise in the postovulatory follicle until after oviposition (van Tienhoven 1980; Poyser and Pharm 1981; Johnson 1986a). Exogenous doses of prostaglandins are potent stimulants of oviposition (Hertelendy et al. 1974; Hargrove and Ottinger 1991). Because many hormonal interactions in cranes are unknown, **hormone therapy** is **not recommended** without extensive laboratory support.

Incubation

Cranes need about four months to complete the nesting cycle. **Nest building** begins a few days before egg production in the female crane and may start even earlier in the male. The endocrine events leading to nest building include increasing levels of FSH and LH, estrogen, progesterone, and prolactin (Cheng 1974, 1979; Cheng and Balthazart 1982; Bluhm et al. 1983). Males and females may both build nests if in separate pens. Unmated wild birds may also build nests (Gee, personal observation). When given a choice of materials, male Sandhill Cranes at Patuxent build coarser, looser nests than females. Nest building often continues after egg laying if stimulated by rising water levels. Sometimes nests become extensive, floating platforms. However, if water levels rise too rapidly, Sandhill Cranes will abandon the submerged nest (P. W. Skyes, Jr., USFWS, Athens, Georgia, and S. A. Nesbitt, Florida Game and Fresh Water Fish Commission, Gainesville, Florida, personal communications).

Both sexes incubate the eggs (Walkinshaw 1965). In incubating birds **prolactin levels rise** and most of the other reproductive hormone levels decline. The metabolic clearance rate of some of the reproductive hormones may increase at the same time due to **increases in thyroid activity** (Jallageas and Assenmacher 1974; Kar and Chandola 1985). Although some feathers may be lost during the incubation period (see Molt section in this chapter), cranes do not develop a brood patch. Egg production normally stops after incubation begins, however, captive Sandhill Cranes that have been brooding chicks can resume egg laying if a chick is removed.

Crane reproductive physiology has received little study. Years of study are necessary to understand the unusual events that occur in captive crane colonies.



Molt

During **molt**, new feathers push out the old. First, **natal down** is replaced or covered by juvenal plumage. The **juvenal plumage** is replaced by **basic plumage** during the first fall and winter. Subsequent molts of the basic plumage follow each year throughout the bird's life. In any one year, feather molts can be complete (all feathers) or incomplete (affecting certain tracts or specific feathers) (Lucas and Stettenheim 1972a, 1972b; Noordhuis 1989).

In cranes, contour feathers emerge during the first two months. First, the primary remiges (large feathers of the hand) emerge, then the secondaries (large feathers on the ulna, elbow, and upper arm) and rectrices (tail), and within the next 2-3 weeks the body contour feathers grow, completing the juvenal plumage. The natal down clings to the tips of the emerging contour feathers for a few weeks before breaking off (Stephenson 1971). Young cranes can fly even before the remiges harden.

Some **immature** cranes need 2 or more **years to completely molt** all juvenal remiges (Lewis 1979; Gee 1981; Layne 1981; Nesbitt 1987; Kaschentseva 1988). However, the body contours and rectrices are probably replaced annually. In Greater Sandhill Cranes, all secondary remiges are replaced in 2.5-year-old birds and all primary remiges in 4.5-year-old birds (Lewis 1979; Gee 1981).

In breeding Whooping Cranes, molt of the basic remiges begins during the incubation period, and most are lost in one or a few days. Breeding Sandhill Cranes molt their remiges during incubation too, but molt may continue for two or more months. Some adult Sandhill Cranes, adult Whooping Cranes, and possibly other species may not complete their molt of remiges every year (Lewis 1979). Cranes do not respond to exogenous hormonal treatments (progesterone thyroxine, and FSH) as do waterfowl, doves and domestic fowl (Payne 1972; Assenmacher and Jallageas 1980; van Tienhoven 1980; Dittami 1981; Gee 1981). However, there may be ways to induce molt using chemical agents or lights. There is some anecdotal evidence that a sudden reduction in artificial photoperiod can induce rapid and extensive molt (S. Haeffner, Denver Zoo, Denver, Colorado, personal communication). The induction of molt on demand would be a useful management tool, but will require more research.

External Factors Controlling Breeding

Crane reproduction can be influenced by a variety of factors such as stress, nutrition, disease, and photoperiod. Increasing or long photoperiod is probably the most influential factor and has been linked to avian reproductive periodicity since the late 1800's (Farner 1986). For reproductively active Sandhill Cranes, gonad weights and testosterone and estrogen levels show a positive correlation with photoperiod (Tacha et al. 1985). The natural photoperiod at temperate latitudes is sufficient to breed all species of cranes in captivity. However, cranes from northern latitudes held captive at temperate latitudes often breed more readily, earlier, and have greater fecundity if provided with an artificially lengthened photoperiod in the early spring (Gee and Pendleton 1992). By extending photoperiod in the spring in the mid-temperature latitude, we can bring together several environmental factors favoring reproduction (see Chapter 3).

A variety of **stressors**, such as disease, inclement weather, moves to new pens, intraspecific conflict, and human activities, can **interfere with the onset and maintenance of reproduction** (Mirande et al. 1988 unpubl.). In birds, disturbance can cause a variety of physiological and behavioral changes that result in stress (Marshall 1961a, 1961b; Ghosh and Banerjee 1983). The most conspicuous stress effect in birds is an elevation of plasma **corticosterone** levels (Siegel 1971; Dittami 1981; Deviche 1983; Dufty and Wingfield 1986) and a suppression of LHRH releases (Bluhm et al. 1983) which in turn disrupt the endocrine balance responsible for regeneration of the reproductive tract, ovulation and other reproductive functions (van Tienhoven 1980; Deviche 1983; Ghosh and Banerjee 1983). By contrast, cyclical variations of low levels of corticosterone are essential to the ovulatory cycle (Follett and Davies 1979; Peczely and Pethes 1980; van Tienhoven 1980; Peczely 1985). How stress affects the crane reproductive effort and how it can be accommodated needs more study.

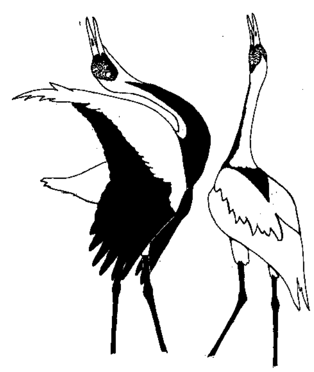
Conclusions

Although the **general pattern** of avian physiology **applies** to cranes, we have identified many physiological mechanisms (e.g., effects of disturbance) that need further study. Studies with cranes are expensive compared to those done with domestic fowl because of the **crane's larger size**, **low reproductive rate**, and **delayed sexual maturity**.

To summarize, the crane reproductive system is composed of physiological and anatomical elements whose function is controlled by an **integrated neural-endocrine system**. Males generally produce semen at a younger age than when females lay eggs. Eggs are laid in clutches of two (1 to 3), and females will lay additional clutches if the preceding clutches are removed.

Both sexes build **nests and incubate** the eggs. **Molt** begins during incubation and body molt may be completed annually in breeding pairs. However, remiges are replaced sequentially over 2 to 3 years, or abruptly every 2 to 3 years in other species. Most immature birds replace their juvenal remiges over a 2 to 3 year period.

Stress interferes with reproduction in cranes by reducing egg production or terminating the reproductive effort. In other birds, stress elevates corticosterone levels and decreases LHRH release. We know little about the physiological response of cranes to stress.



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